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The Regional Vegetational History of the High Peaks (Adirondack Mountains), New York

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By Donald R. Whitehead
and Stephen T. Jackson



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THE REGIONAL VEGETATIONAL HISTORY OF THE HIGH PEAKS (ADIRONDACK MOUNTAINS) NEW YORK

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ABSTRACT

We completed palynological investigations of four lake sites along an elevation gradient (661 to 1320 m) in the High Peaks region of the Adirondack Mountains of New York (U.S.A.). Our studies provide a record of the regional vegetational history of the east-central Adirondacks.

The overall vegetational and climatic changes inferred for the High Peaks are similar to those elsewhere in the Northeast. However, there are significant differences in the timing and order of arrival of many taxa. These differences may result from the rugged topography and isolated position of the Adirondacks, or from climatic and edaphic variations among regions.

The High Peaks region was deglaciated approximately 13,000 yr BP. From ice retreat until about 12,000 yr BP the vegetation at all elevations was dominated by herbs and probably consisted of tundra. *Picea* was the first tree taxon to immigrate (prior to 12,000 yr BP at low elevations), and *Picea*-dominated woodlands were well-established at all elevations below 1200 m by 12,000 yr BP. *Picea* declined rapidly at all elevations beginning at about 10,500 yr BP. An expansion of *Alnus* populations (*Alnus crispa*) accompanied the *Picea* decline. This *Alnus* maximum is more pronounced at high elevations. *Populus* also immigrated at this time, and *Larix* and *Abies* populations expanded.

The early Holocene was characterized by the increasing importance of *Betula* (probably *Betula papyrifera*), the immigration and rapid expansion of *Pinus strobus* (about 9500 yr BP), and the subsequent arrival and spread of *Acer saccharum*, *Tsuga*, and *Fagus* between 9700 and 7000 B.P. Mixed conifer-hardwood forests became established. *Pinus strobus*, *Tsuga* and most deciduous taxa were more abundant at low-elevation sites; *Abies* and *Betula* were more common at high-elevation sites.

By about 7000 yr BP, *Pinus strobus* had decreased in abundance, and *Tsuga* dominated forests with *Pinus strobus*, and hardwoods became established at low-elevation sites. *Abies* and *Betula* continued to dominate at higher elevations.

Forests at lower elevations experienced significant changes at 4800 yr BP. *Tsuga* declined abruptly, perhaps because of a pathogen, and *Betula* (probably *Betula lutea*), *Acer saccharum*, *Acer pensylvanicum*, and *Fagus* increased. Thus, low-elevation sites shifted from conifer dominance to hardwood dominance, while *Betula* and *Abies* remained dominant at high elevations. *Tsuga* began to recover by about 3400 yr BP and expanded at low elevations. *Picea* began to expand again about 2000 yr BP. The existing vegetation zones became established within the past 2000 years. *Tsuga*, *Fagus*, and *Acer saccharum* appear to have decreased in abundance at low elevations during this time interval.

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INTRODUCTION

Well-dated pollen and macrofossil studies in the upper Midwest and the Northeast have provided detailed information concerning the patterns of vegetational and climatic change since deglaciation (for example, M.B. Davis 1969, 1981b, Williams 1974, Brubaker 1975, R.B. Davis *et al.* 1975, Spear and Miller 1976, Whitehead 1979, Miller and Thompson 1979, Spear 1981, Anderson *et al.* 1986, Overpeck 1985). This large data base has provided valuable insights concerning the composition of past plant communities, the dynamics of vegetation, and the responses of forest types and individual taxa to inferred climatic change at a subcontinental scale (M.B. Davis 1976, 1981b, 1983; Bernabo and Webb 1977; M.B. Davis *et al.* 1980; Webb *et al.* 1983; R.B. Davis and Jacobson 1985; Gaudreau and Webb 1985; Webb 1988; Jacobson *et al.* 1987; Delcourt and Delcourt 1987).

Although the spatial and temporal vegetation patterns in the Northeast are now well understood at a subcontinental scale (M.B. Davis *et al.* 1980, Gaudreau and Webb 1985, Ritchie 1987, Webb 1988), significant geographic gaps and a number of unresolved questions still exist. For example, little is known about the Late-Pleistocene and Holocene environmental history of the Adirondack region of upstate New York (Fig. 1), a vast area with varied topography, climate, soils, and vegetation. Few paleoecological studies have been carried out, although the region has many lakes that might contain sedi-

ments suitable for pollen analysis. The general trends in the Adirondacks may differ from those inferred elsewhere in northeastern North America owing to its geographic position and the unique characteristics of its bedrock, soils, topography, and climate. In addition, for much of the late-glacial and early Holocene, the Adirondack region was isolated as a broad, rugged peninsula, separated from New England by the Champlain Sea and proglacial lakes, from the north by ice, the Champlain Sea and other proglacial lakes, and from the west by high-water stages of glacial Lake Ontario (Prest 1970, Denton and Hughes 1981). This isolated position, combined with the rugged topography, might have influenced the immigration of species and resulted in a unique sequence of vegetational changes.

This paper focuses on the High Peaks region of the Adirondacks and is designed to explore: (1) the general sequence of vegetational changes for the region, (2) the altitudinal patterns of vegetational change, (3) the immigration history of the dominant forest trees, (4) evidence for responses of vegetation to Holocene climatic changes, (5) the response of Adirondack forests to the abrupt mid-Holocene (4800 yr BP) regional decline of *Tsuga*, and (6) the patterns of forest change associated with expansion of *Picea* in the late Holocene. The investigation is based on palynological analyses of cores from four lakes ranging in elevation from 661 to 1320 m.

REGIONAL SETTING

Geology

The Adirondack Mountains form a large, highly dissected geologic dome in northeastern New York. The bedrock consists of a variety of Proterozoic metamorphic and igneous rocks, primarily anorthosite, and charnockitic gneiss (Budington 1953). Maximum elevation and relief (300 m - 1500 m) are attained in the High Peaks region in the northeastern portion of the dome (Fig. 1).

Following the St. Pierre Interstade, the Adirondacks were covered by continental ice (about 55,000 yr BP) that probably persisted without interruption until the Late Woodfordian. Deglaciation of the High Peaks probably began during either the Erie (about 15,000 yr BP) or the Mackinaw Interstade (about 14,000 yr BP) (Connally and Sirkin 1971, 1973, Craft 1979). The age of the recessional moraine complex near Loon Lake (35 km north of the High Peaks) is about 12,700 yr BP (Denny 1974). With the exception of localized stagnant ice, the High Peaks were probably free of ice before 12,500 yr BP.

Soils

Soil types in the High Peaks are similar to those described on Whiteface Mountain, an anorthosite/charnockite massif 25 km N of the High Peaks (Witty 1968, Witty and Arnold 1970). Witty (1968) recognized three primary soil groups: histosols, haplohumods, and cryohumods. The latter two soil types are spodosols. On Whiteface, the haplohumods are moderately deep to deep, well-drained, stony, coarse-textured soils formed in till at low elevations. Today these soils support hardwood and pine forests (Witty 1968). Cryohumods are shallow to deep, well-drained, generally coarse-textured soils formed in till or congelifracate, and they support *Picea-Abies* and *Abies* forests (> 800 m) (Witty 1968). The histosols are organic soils consisting almost entirely of partially decomposed plant material (Brady 1974, Cline and Marshall 1977). On Whiteface they support *Picea-Abies* and *Abies* forests (> 800 m). These soils occur on bedrock and boulder slopes, summits, and poorly drained saddles and depressions (Witty 1968, Witty and Arnold 1970).

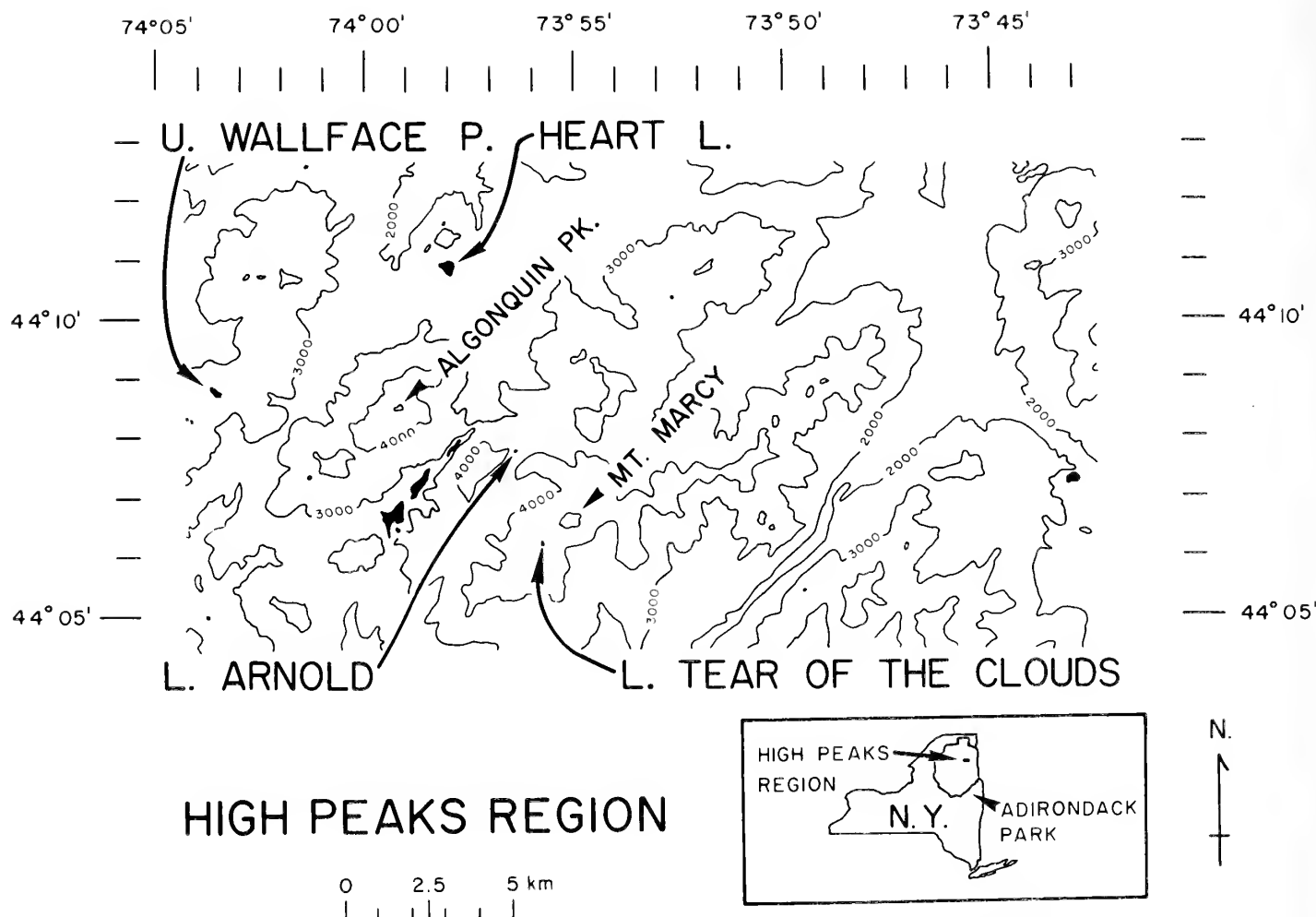


Figure 1. Map of the High Peaks Region of the Adirondacks illustrating location of the four lake sites.

Climate

Climate of the Adirondack region is characterized by cold, snowy winters and cool, wet summers (Mordoff 1949). Precipitation is distributed more or less evenly throughout the year; droughts are rare (Dethier 1966).

Significant local climatic variations occur in the High Peaks area (Kudish 1975, Jackson 1989). Temperature and length of frost-free season decrease and precipitation and snowfall increase with elevation. Elevational lapse rates for these variables are available in Kudish (1975) and Jackson (1990). Fog precipitation, rime icing, cloud cover, and wind speed also increase with elevation.

Vegetation

The vegetation of the Adirondack Mountains is arranged in a series of altitudinal zones, ranging from *Quercus-Carya* for-

est at low elevations along Lake Champlain to alpine tundra on the highest summits in the High Peaks region (Braun, 1950, Bray, 1915). In order of increasing elevation, the zones are (1) temperate hardwoods-northern hardwoods-*Tsuga-Pinus* forest (< 300 m), (2) mixed conifer-northern hardwoods forest (300-850 m), (3) subalpine *Picea-Abies-Betula papyrifera* forest (850-1200 m), (4) subalpine *Abies* forest (1200-1450 m), and (5) alpine tundra (> 1450 m). The transitions between adjacent zones are gradual and are not well-defined. Within each zone there are important secondary patterns that result from variations in soil texture, soil moisture, microclimate, slope, aspect, and disturbance history (Braun 1950, DiNunzio 1972, Heimberger 1934, Holway *et al.* 1969, Kudish 1975, 1981, Nicholson *et al.* 1979, Reiners and Lang 1979, Scott and Holway 1969, Sprugel 1976, Young 1934). For a more detailed description of vegetation see Jackson (1990).

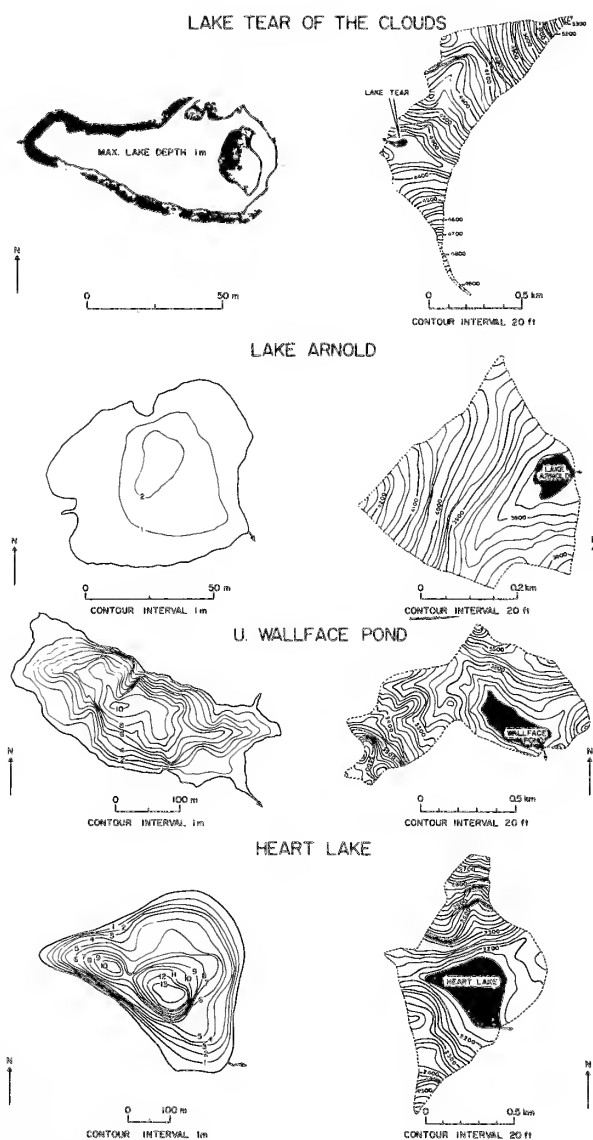


Figure 2. Morphometric and watershed maps of the sites.

SITE DESCRIPTIONS

All of the basins (Fig. 2, Table 1) appear to have been formed by glacial erosion of anorthosite bedrock. Each basin has a single outlet flowing over bedrock. Jackson (1990) provides detailed descriptions of the study sites and their watersheds.

Heart Lake (661 m)

Bouldery, sandy tills are the predominant parent material in the Heart L. watershed. Bedrock outcrops and talus occur on steep slopes. The watershed is entirely within the mixed conifer-northern hardwoods forest zone.

The entire watershed was burned in 1903 (Suter 1904). The steep slopes of the northern part of the watershed are dominated by *Betula papyrifera* and *Populus tremuloides*. Slopes in the southwest portion of the watershed were burned less severely and support relatively mature stands of *Fagus*, *Acer saccharum*, *Betula lutea*, and *Betula papyrifera*. The eastern portion of the watershed is disturbed by buildings, campsites, and access roads.

Upper Wallface Pond (948 m)

Mineral soils in the Upper Wallface Pond watershed are formed in shallow, leached, sandy substrates and are restricted to relatively flat areas. Histosols occur where there is no fine-

grained material mantling the bedrock. The watershed is within the subalpine *Picea-Abies-Betula papyrifera* forest zone.

Lake Arnold (1150 m)

Mineral soils in the Lake Arnold watershed are formed in congelifRACTate, and most are < 15 cm thick. Lithic borofolists are extensive in the watershed; saturated histosols occur locally. A small, non-forested wetland is situated on the southwest shore of the pond. Vegetation of the watershed is a mosaic of mature *Picea-Abies* stands and dense stands of young *Abies*; *Betula papyrifera* and some *Pyrus americana* occur locally.

Lake Tear of the Clouds (1320 m)

Lake Tear of the Clouds is located in a col between Mt. Skylight and Mt. Marcy. An extensive open wetland borders the lake's east end through which a permanent tributary stream flows. The watershed is within the subalpine *Abies* zone and may extend into the alpine tundra zone on Mt. Skylight and Mt. Marcy. *Abies balsamea* is the dominant tree species; *Betula papyrifera* is locally important. *Picea rubens* is rare. Fir waves (Sprugel 1976, Reiners and Lang 1979) are frequent on the steeper slopes.

Table 1

Site Characteristics

SITE	COORDINATES		ELEVATION (m)	SURFACE AREA (ha)	MAXIMUM DEPTH (m)	MEAN DEPTH (m)	WATERSHED AREA (ha)	MEAN HYDROLOGIC
	LATITUDE	LONGITUDE						RETENTION TIME (yrs)
Heart Lake	44°10'50"N	73°58'03"W	661	11.2	13.5	5.2	55.9	1.9
Upper Wallface Pond	44°08'47"N	74°03'15"W	948	5.5	9.0	3.8	58.3	0.4
Lake Arnold	44°07'45"N	73°56'25"W	1150	0.4	2.5	0.9	13.7	0.03
Lake Tear of the Clouds	44°06'15"N	73°55'55"W	1320	0.4	0.8	0.4	40.2	0.003

FIELD METHODS

All cores were taken from the deepest point in the lake with a 5 cm diameter Wright-Cushing square-rod piston sampler (Cushing and Wright 1965). Two parallel sequences of meter-length core segments were taken at Heart Lake, Upper Wallface Pond, and Lake Arnold, one starting at the mud-water interface, and a second at a depth of 0.5 m in the sediment. A duplicate top-meter core (i.e., 0-1.0 m) was also

taken. A single core was obtained from Lake Tear of the Clouds.

Cores were extruded in the field, measured and described, wrapped in Saran Wrap and aluminum foil, and placed in aluminum liners for shipment to Indiana. The cores were then stored at 4°C until analyzed. Top meter cores were kept in the coring tubes for return to the laboratory.

LABORATORY METHODS

In the laboratory, core segments were remeasured and redescribed stratigraphically. Color, texture, consistency, presence of macrofossils, and abundance of clasts were recorded.

Volumetric subsamples for analyses of pollen, diatoms, sediment chemistry, and loss on ignition were obtained from each core. Disks one cm thick were sliced from the cores at 5-cm intervals. A brass punch was used to extract cylindrical subsamples (1.0 cm³) from the interior of each disk.

Samples for pollen analysis were processed so that calculations of net accumulation rates could be made. The 1.0 cm³ pollen subsample was prepared using standard techniques (Faegri and Iversen 1975) (treatment with 10% KOH, 10% HCl, concentrated HF, and acetolysis).

Pollen counts were made at a magnification of 400× with a Leitz Orthoplan microscope. Difficult grains were studied under oil immersion (1000×). At least 500 grains were counted for most levels. Counts from which accumulation

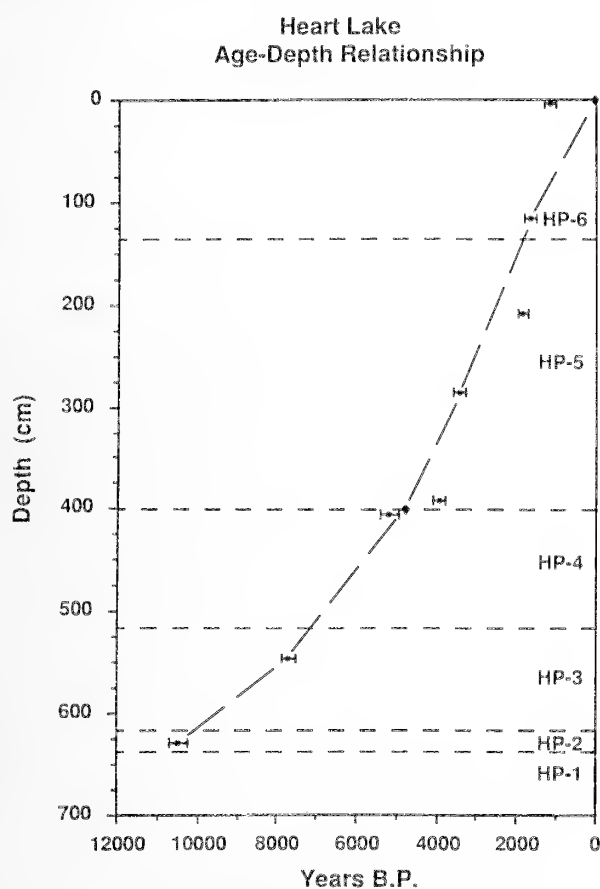


Figure 3. Heart Lake. ¹⁴C dates vs. Depth.

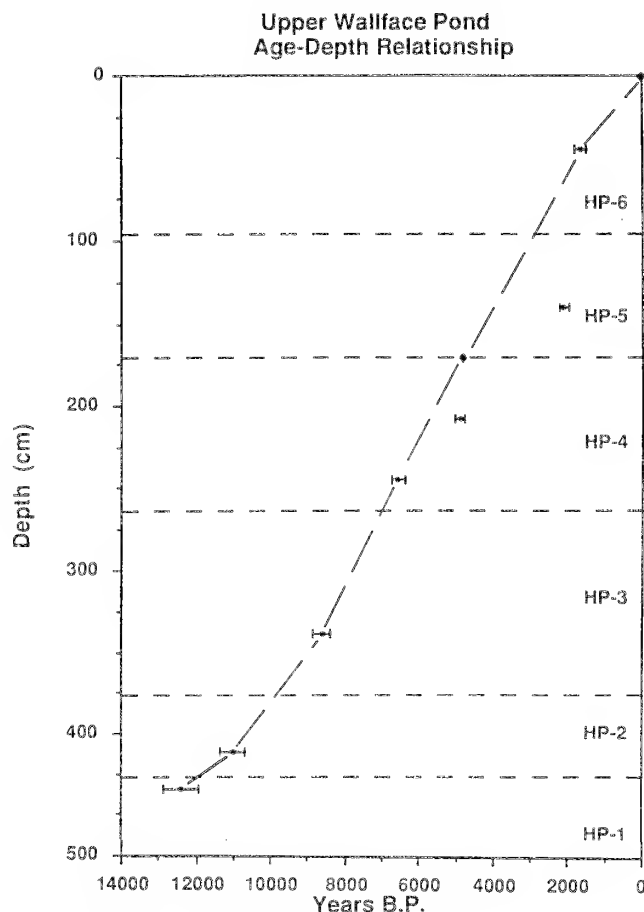


Figure 4. Upper Wallface Pond. ¹⁴C dates vs. Depth.

rates could be calculated were made by tabulating all pollen and spore types that were encountered on parallel, slightly overlapping transects on the entire slide. Percentage counts were made on parallel, evenly spaced transects. In this case, either half or all of the slide was counted.

The pollen sum used for calculating percentages included all identified pollen types except those of obligate aquatic macrophytes. Spores were not included in the pollen sum.

Measurements of diploxylon-type *Pinus* and *Betula* pollen were made at selected levels from the Lake Arnold core (Figs. 15 and 16). Measurements were made at 400 \times . Corpus length was the variable measured on *Pinus* grains.

Subsamples of about 5 cm length were taken at selected intervals for ^{14}C dating. In general, these samples included the base of the core, the mud-water interface, and critical pollen zone boundaries. Samples were dated by Geochron Laboratories and the Radiocarbon Laboratory of the Smithsonian Institution.

Pollen assemblage zones were defined to facilitate vegetational and climatic reconstructions. Qualitative (significant maxima, minima, and general trends) and quantitative techniques were employed. Stratigraphically constrained cluster analysis was performed using OPTAGG1 (E. J. Cushing, per. comm.)

RESULTS

Radiocarbon Chronology

The radiocarbon dates from the four sites are presented in Table 2, and the age-depth relationships for the four cores are indicated in Figs. 3-6. Age models were derived by linear interpolation of radiocarbon dates. We also used the mud-water interface (assumed to be 0 yr BP) and the *Tsuga* pollen decline (assumed to be 4800 yr BP) (Davis 1981, Webb 1982) at each site as points in the interpolations.

At Heart Lake, we did not use the surface date (1160 ± 150 yr BP), which is impossibly old for a softwater lake (pH in 1979-1980 was 6.6 (Charles 1982)). We have no explanation for this anomalous date. We also did not use the date of 1850 ± 120 yr BP or the two dates adjacent to the *Tsuga* decline in the interpolation (Fig. 3).

The age model for Upper Wallface Pond was based on the topmost ^{14}C date (1635 ± 155 yr BP), the lower four ^{14}C

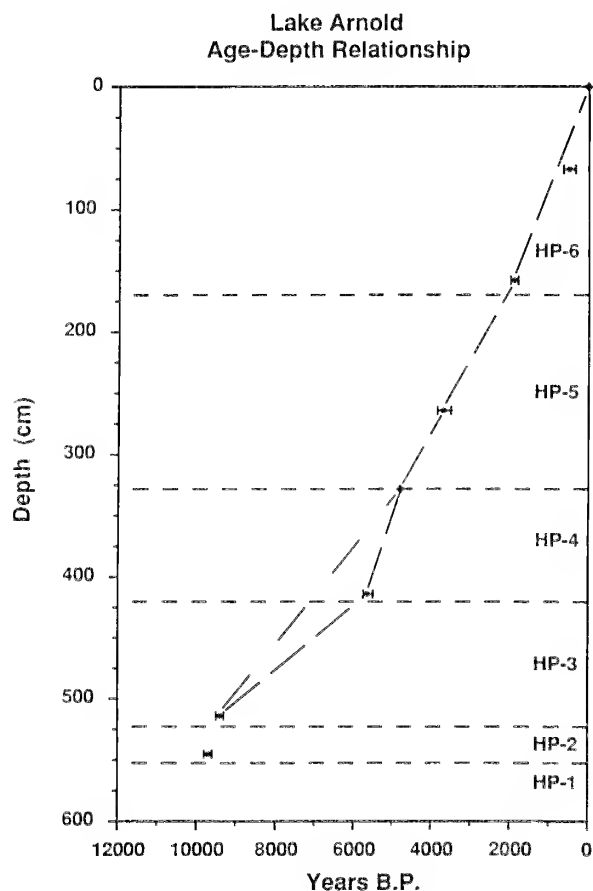


Figure 5. Lake Arnold. ^{14}C dates vs. Depth.

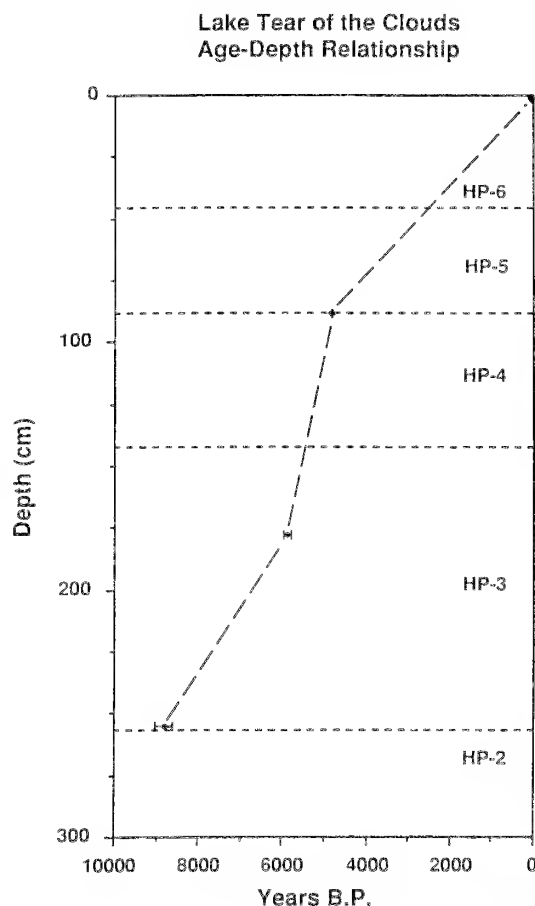


Figure 6. Lake Tear of the Clouds. ^{14}C dates vs. Depth.

Table 2

Radiocarbon Dates-Adirondack Sites

Site	Depth Interval (cm)	Date	Sample Number
Heart Lake	0-7	1160±150	GX-4575
	113-118	1670±150	GX-5367
	206-211	1850±120	GX-4576
	283-288	3440±165	GX-5368
	388-393	3935±165	GX-4577
	403-408	5175±215	GX-5369
	543-548	7695±195	GX-5370
	627-632	10,475±230	GX-4578
Upper Wallface Pond	42.5-46.5	1635±155	GX-5372
	138-142	2105±140	GX-5373
	205-211	4900±155	SI-4390
	242.5-246.5	6580±185	GX-5374
	337-341	8630±240	GX-5375
	409-413	11,015±320	GX-5376
	429.5-438	12,390±480	GX-5377
Lake Arnold	65-70	505±150	SI-4392
	156-161	1910±100	SI-4393
	261-266	3675±160	SI-4394
	411-416	5630±120	SI-4397
	511-516	9415±105	SI-4397
	543-548	9710±105	SI-4398
Lake Tear of the Clouds	175-180	5865±90	SI-4387
	252-258	8815±220	SI-4388

dates, the *Tsuga* decline, and the mud-water interface (Fig. 4). Two ^{14}C dates (2105 ± 140 and 4900 ± 155 yr BP) appear anomalously young.

The lowest radiocarbon date at Lake Arnold appeared to be too young and was not used in the age model. We derived two alternative age models for Lake Arnold, one that incorporated the radiocarbon date of 5630 ± 120 yr BP and one that did not (Fig. 5). Jackson (1989) and Jackson and Whitehead (1990) used the age model that included this date.

Dating of the core from Lake Tear of the Clouds is uncertain because we have only two ^{14}C dates and because there are several breaks in the core (Figs. 6 and 13). There are also changes in sediment type, suggesting changes (including possible hiatuses) in sedimentation rate of this small subalpine basin. We assumed continuous deposition and used both ^{14}C dates along with the *Tsuga* decline and the sediment surface in the age model (Fig. 6).

Sediment accumulation rates were calculated at each sampling interval for the Heart Lake and Upper Wallface long cores. These accumulation rates were then used to derive total pollen accumulation rates.

Pollen Stratigraphy

Pollen sequences for each of the sites are presented in Figs. 7-14. Our zone designations (HP-1 to HP-6; HP = High Peaks) are intended to apply only to the High Peaks area. Pollen stratigraphic changes detected in the four diagrams are comparable and thus representative of the High Peaks region, but they may differ somewhat in both age and pollen percentages from those in other parts of the Adirondacks (e.g., Overpeck 1985) and elsewhere in the Northeast. Zones HP-1 to HP-6 are equivalent in a very general way to the classic pollen assemblage zones recognized in the Northeast (T, A, B, C1-C3) (Deevey 1939, Davis 1969, Whitehead 1979, Gaudreau and Webb 1985). The horizontal percentage scales in the pollen diagrams (Figs. 7-14) differ from pollen type to pollen type.

Zone HP-1: Herb-*Pinus* Assemblage Zone

This zone spans the time interval from glacial retreat ($> 12,500$ yr BP) to approximately 12,000 yr BP, and it is repre-

HEART LAKE ARBOREAL POLLEN

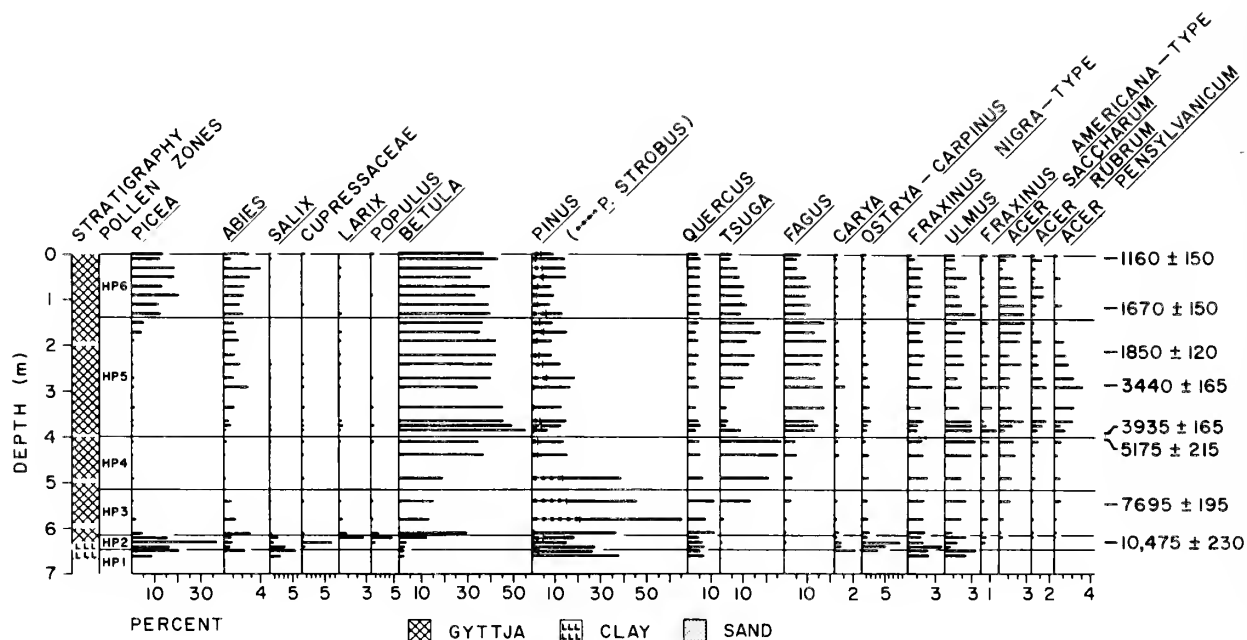


Figure 7. Heart Lake. Pollen Diagram: Arboreal pollen.

HEART LAKE SHRUBS, HERBS, & MISCELLANEOUS

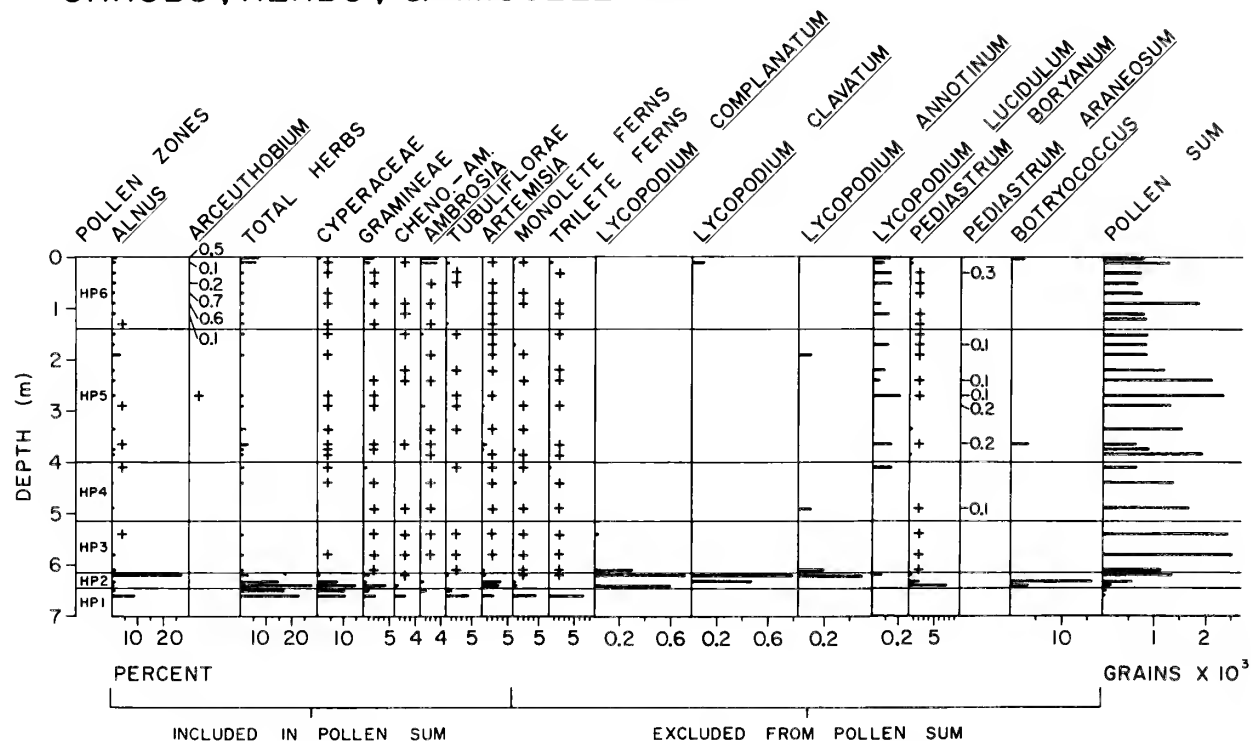


Figure 8. Heart Lake. Pollen Diagram: Shrubs, herbs, and miscellaneous.

sented at all of the study sites except Lake Tear of the Clouds. It is characterized by high percentages of herb (20%), *Picea* (> 10%), and *Pinus* (> 20%) pollen. Low percentages of some deciduous tree taxa (*Betula*, *Quercus*, *Carya*, *Ostrya-Carpinus*, *Fraxinus nigra*-type, and *Ulmus*) generally coincide with slight maxima for *Salix* and "Cupressaceae" -type in the upper levels of the zone. *Alnus* is represented, but its percentages are low. The *Pinus* pollen consists entirely of small diploxylon grains. Similarly, the *Betula* pollen is small and thus likely to represent dwarf *Betula* (Fig. 16). The herb pollen is predominantly sedge and grass. There are distinct maxima for *Ambrosia*, *Artemisia*, *Rumex*, and *Tubuliflorae*-type. Grains of putative tundra taxa occur (e.g., *Empetrum*, *Saxifraga* cf. *oppositifolia*, *Salix* cf. *herbacea*, *Lycopodium selago*, and a variety of caryophylls). The overall pollen influx is low (< 500 grains cm⁻² yr⁻¹).

Zone HP-2: *Picea* Assemblage Zone

The time span of this zone is from about 12,000 to 9700 yr BP. The lower zone boundary (HP-1/HP-2) is delimited primarily on the basis of increasing percentages of *Picea* and decreasing percentages of herbs and *Pinus*. The upper zone boundary (HP-2/HP-3) is distinguished by a steep decline of *Picea*, the *Alnus* maximum, a sharp increase of *Betula*, increasing percentages of pine (now including haploxylon types), and slight maxima for *Larix* and *Populus*.

The most distinctive feature of the zone is a maximum for *Picea* (percentages range from 10-60%). The *Picea* maximum is followed by a sharp decline towards the top of the zone. Percentages of *Abies* and *Betula* are higher than in HP-1 and increase gradually toward the top of HP-2. *Betula* grains are small (Fig. 18). Maxima for *Salix* and "Cupressaceae"-type occur in the lower half of the zone, and maxima for *Larix* and *Populus* occur near the top of the zone. Percentages of *Quercus*, *Carya*, *Ostrya-Carpinus*, *Fraxinus nigra*-type, and *Ulmus* are similar to those in HP-1. *Alnus* begins to increase sharply in the upper half of the zone and attains a maximum close to the HP-2/HP-3 zone boundary.

Herb percentages are high at the base of the zone and decline sharply in the lower half. The types represented are similar to those in HP-1. There are distinct maxima for several species of *Lycopodium* within the zone at Heart Lake (*L. annotinum*, *L. clavatum*, and *L. complanatum*-type).

Pollen accumulation rate increases sharply in this zone from < 500 grains cm⁻² yr⁻¹ to 8000-15,000 grains cm⁻² yr⁻¹ at the top.

Zone HP-3: *Pinus* Assemblage Zone

This assemblage zone spans the time interval from 9700 to 7000 yr BP. The lower zone boundary is defined by a sharp increase in *Betula* and *Pinus* percentages (including *Pinus strobus*), a corresponding decline in *Picea*, an *Alnus* maxi-

**UPPER WALLFACE POND
ARBOREAL POLLEN**

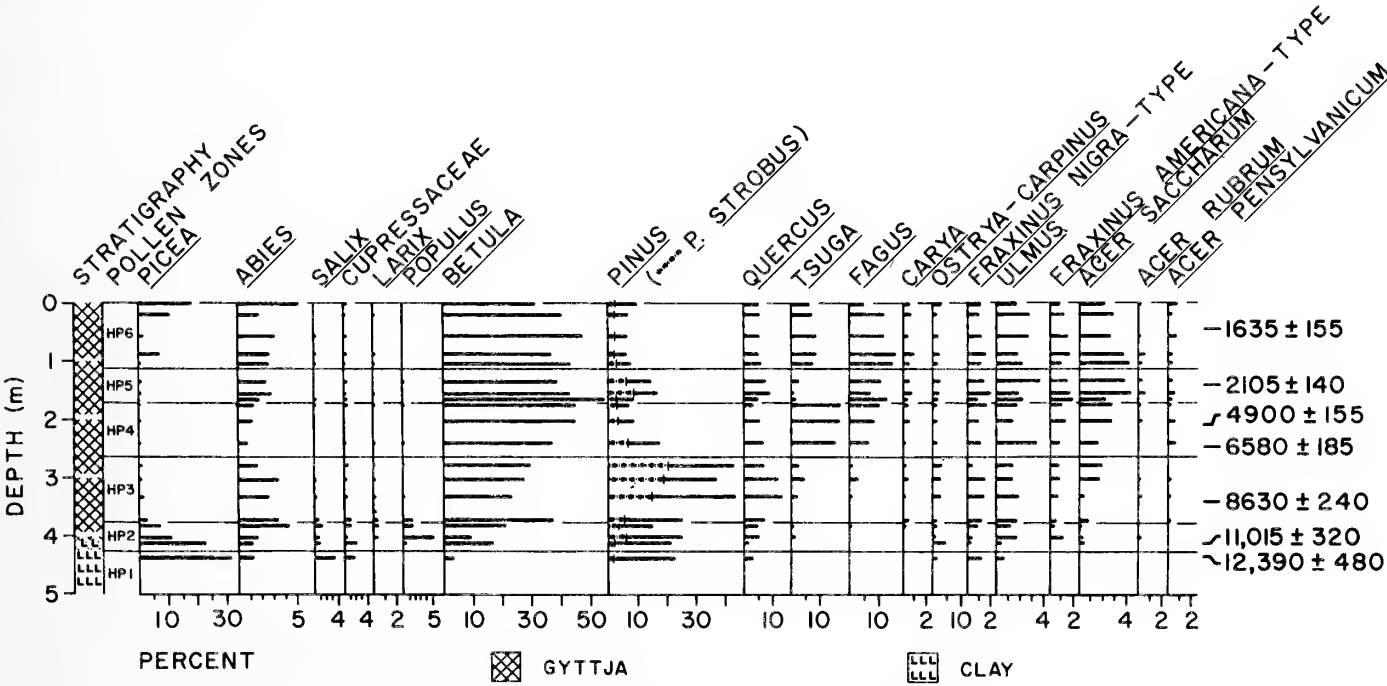


Figure 9. Upper Wallface Pond. Pollen Diagram: Arboreal pollen.

UPPER WALLFACE POND

SHRUBS, HERBS, & MISCELLANEOUS

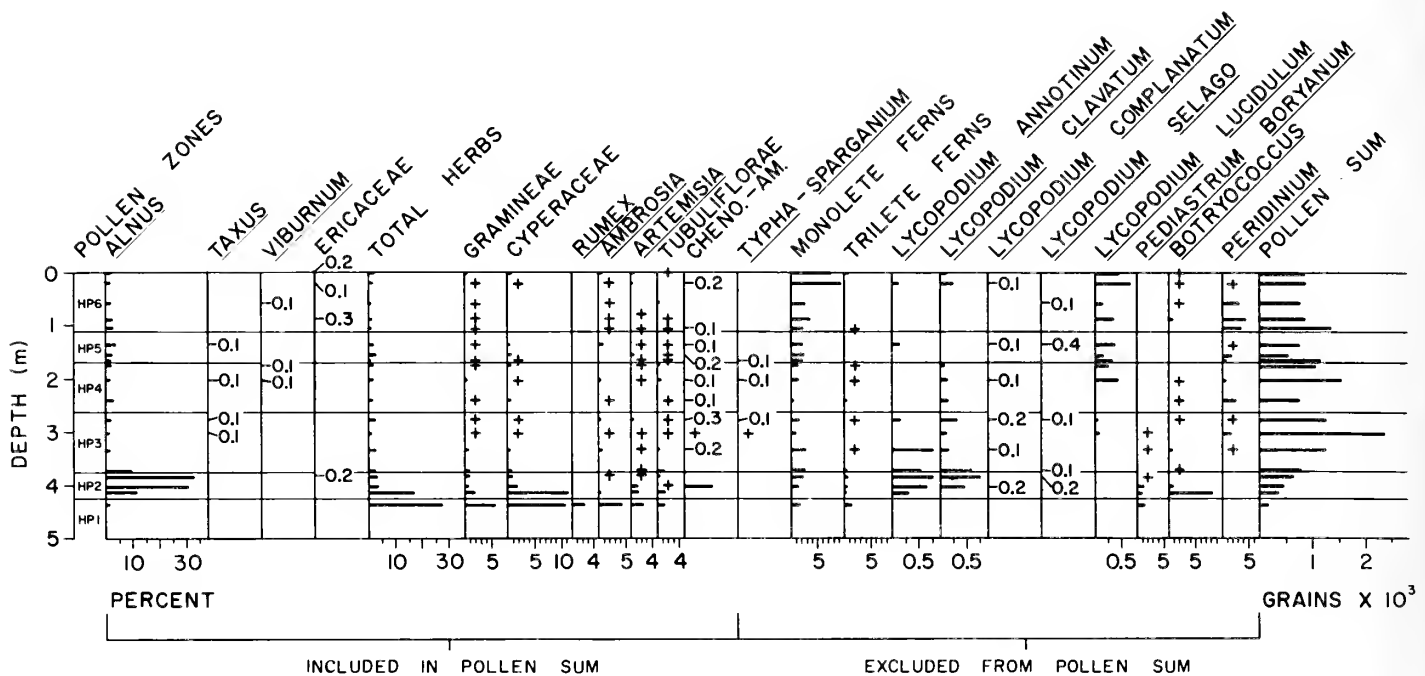


Figure 10. Upper Wallface Pond. Pollen Diagram: Shrubs, herbs, and miscellaneous.

num, and maxima for *Larix* and *Populus*. The upper zone boundary is delimited primarily by the marked decline in *Pinus* percentages and the reciprocal increase in *Tsuga*.

The most characteristic feature of the zone is the pronounced maximum of *Pinus* (up to 60%). A significant fraction of the *Pinus* pollen is of the haploxylon (*Pinus strobus*) type (50% of total *Pinus* and up to 91% of *Pinus* pollen identifiable to haploxylon or diploxylon type). *Betula* percentages are high throughout the zone (often over 30%) and there is a significant maximum at the HP-2/HP-3 transition at all sites except Lake Tear of the Clouds. Although the majority of *Betula* grains are < 20 μ m in diameter, there is an increasing representation of larger (presumably arboreal) grains (Fig. 16). *Tsuga* and *Acer saccharum* appear near the base of the zone and increase steadily thereafter. *Fagus* begins to increase near the top of the zone.

The total pollen accumulation rate is high, up to 25,000 to 30,000 grains $\text{cm}^{-2} \text{yr}^{-1}$. However, it is important to note that the accumulation-rate data from here to the present must be interpreted with caution, as focusing may have had an important influence (M.B. Davis *et al.* 1984).

Zone HP-4: *Tsuga* Assemblage Zone

The *Tsuga* assemblage zone spans the interval 7000 to 4800 yr BP. The lower zone boundary is defined primarily by the increase in *Tsuga* and the reciprocal decrease in *Pinus*. The upper boundary is marked by the sharp decline in *Tsuga* and

increases in *Betula*, *Fagus*, and *Acer saccharum*.

This zone is characterized by a prominent maximum of *Tsuga*, steadily increasing percentages of *Fagus*, *Acer saccharum*, and *Betula*, and declining percentages of *Pinus*. The *Betula* grains are almost exclusively "tree" types. Herb and shrub percentages are low. *Lycopodium lucidulum* spores begin to occur consistently within this zone.

The total pollen accumulation rate varies between 15,000-27,000 grains $\text{cm}^{-2} \text{yr}^{-1}$.

Zone HP-5: *Betula-Fagus* Assemblage Zone

The *Betula-Fagus* zone occurs between 4800 and 2000 yr BP.

The HP-4/HP-5 zone boundary is defined by a sharp decline in *Tsuga* percentages, and the upper zone boundary by a distinct increase in *Picea* percentages.

The zone is characterized by high percentages of *Betula* (40-60%) and maxima for *Fagus*, *Acer saccharum*, *Acer pensylvanicum*, and *Abies*. *Tsuga* percentages are low before 3400 yr BP.

Pollen accumulation rate in this zone varies erratically between 5000-45,000 grains $\text{cm}^{-2} \text{yr}^{-1}$.

Zone HP-6: *Picea-Betula* Assemblage Zone

The *Picea-Betula* zone extends from approximately 2000 yr BP to the present. The most characteristic features of the zone

LAKE ARNOLD ARBOREAL POLLEN

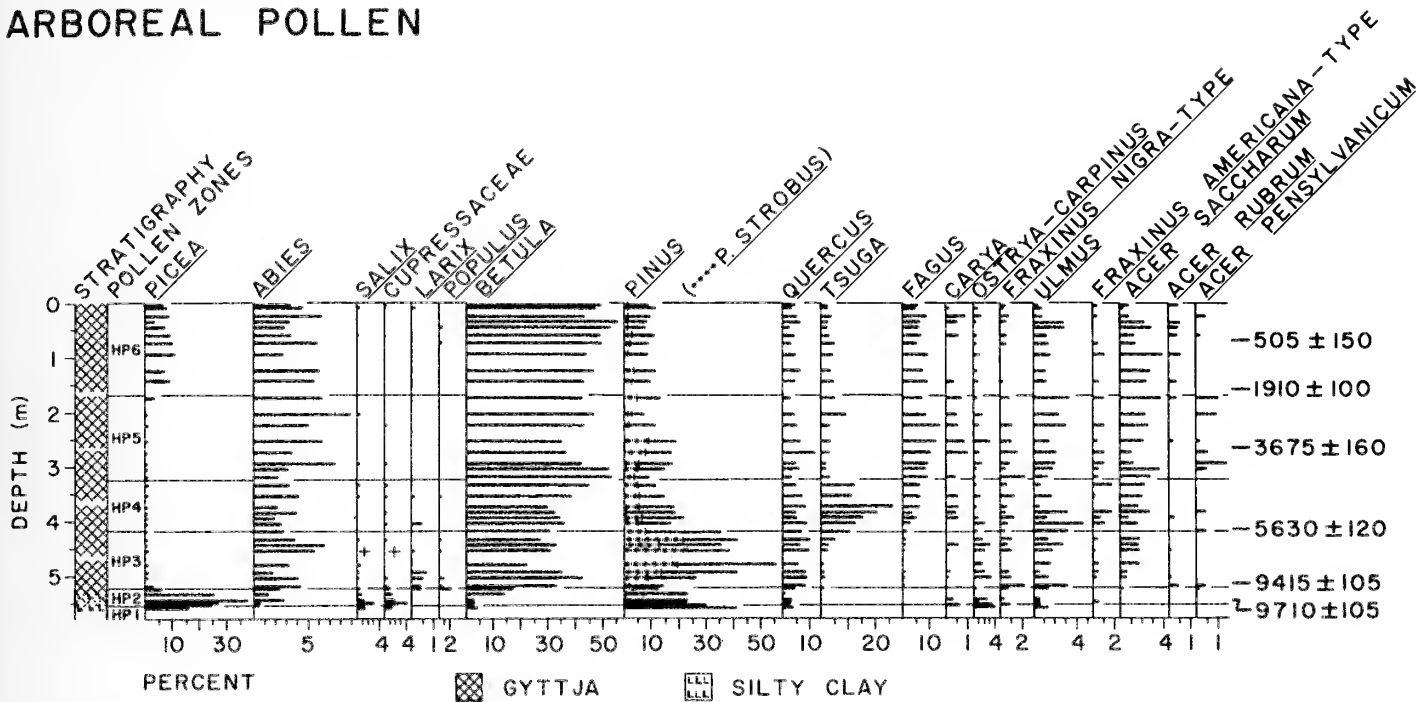


Figure 11. Lake Arnold. Pollen Diagram: Arboreal pollen.

are the increase in *Picea* percentages, which marks the lower zone boundary, and the high *Picea* percentages throughout the remainder of the zone (percentages range from 10-20%). *Betula* percentages are also high throughout. *Abies* percentages tend to be even higher than in HP-5. *Tsuga*, *Fagus*, and *Acer saccharum* decline gradually throughout the zone.

The uppermost spectra of the zone are characterized by distinct increases in herb percentages, including *Ambrosia*, *Tubuliflorae*, grasses, and other weedy taxa such as *Plantago*.

Pollen accumulation rate in this zone varies between 5-45,000 grains $\text{cm}^{-2} \text{yr}^{-1}$.

Variability among sites

Because the four sites span a significant range of elevations and differ in lake-surface areas, watershed characteristics, soils, and present vegetation, pollen spectra are expected to vary among sites. The following taxa display elevational patterns probably caused by differences in local vegetation.

Abies: Percentages for *Abies* are generally lowest at Heart Lake and increase with elevation. For example, in Zone HP-3, *Abies* percentages at Heart Lake range from 1-2%, at Wallface from 2-3%, at Lake Arnold from 3-6%, and at Lake Tear of the Clouds from 3-7%. This elevational trend is evident throughout the Holocene.

Betula: *Betula* percentages increase with elevation through Zones HP-2, HP-3, and HP-4. This trend is also present during

the latter portion of the Holocene, although more weakly. The highest *Betula* percentages (53%) are associated with the *Tsuga* decline (HP-4/HP-5 zone boundary) in the Heart and Wallface profiles.

Tsuga: *Tsuga* percentages show a strong elevational trend, with highest percentages at Heart Lake. This is evident during the initial rise of *Tsuga* (in Zone HP-3), during the entire *Tsuga* zone (HP-4), and in the late Holocene (post-3400 yr BP) after the "recovery" of *Tsuga*.

Fagus: The elevational pattern for *Fagus* is similar to that for *Tsuga*, although less dramatic.

Ostrya-Carpinus: The peak of *Ostrya-Carpinus* pollen at the base of Zone HP-2 appears to have an elevational trend, with percentages higher at lower-elevation sites.

Acer: Although the percentages for *Acer saccharum*, *Acer rubrum*, and *Acer pensylvanicum* are always low, they are consistently higher in profiles from sites at lower elevations.

Alnus: A strong elevational trend is associated with the *Alnus* peak that spans the HP-2/HP-3 zone boundary. *Alnus* percentages are markedly higher at the higher elevation sites. In addition, the *Alnus* maximum persists longer in Zone HP-3 at the higher sites.

Monolete Fern Spores: There is a steady increase in the percentage of monolete spores throughout the Holocene at all sites. A sharp elevational gradient also exists. Fern spores are much more frequent at Lake Arnold and Lake Tear of the Clouds.

LAKE ARNOLD

SHRUBS, HERBS, & MISCELLANEOUS

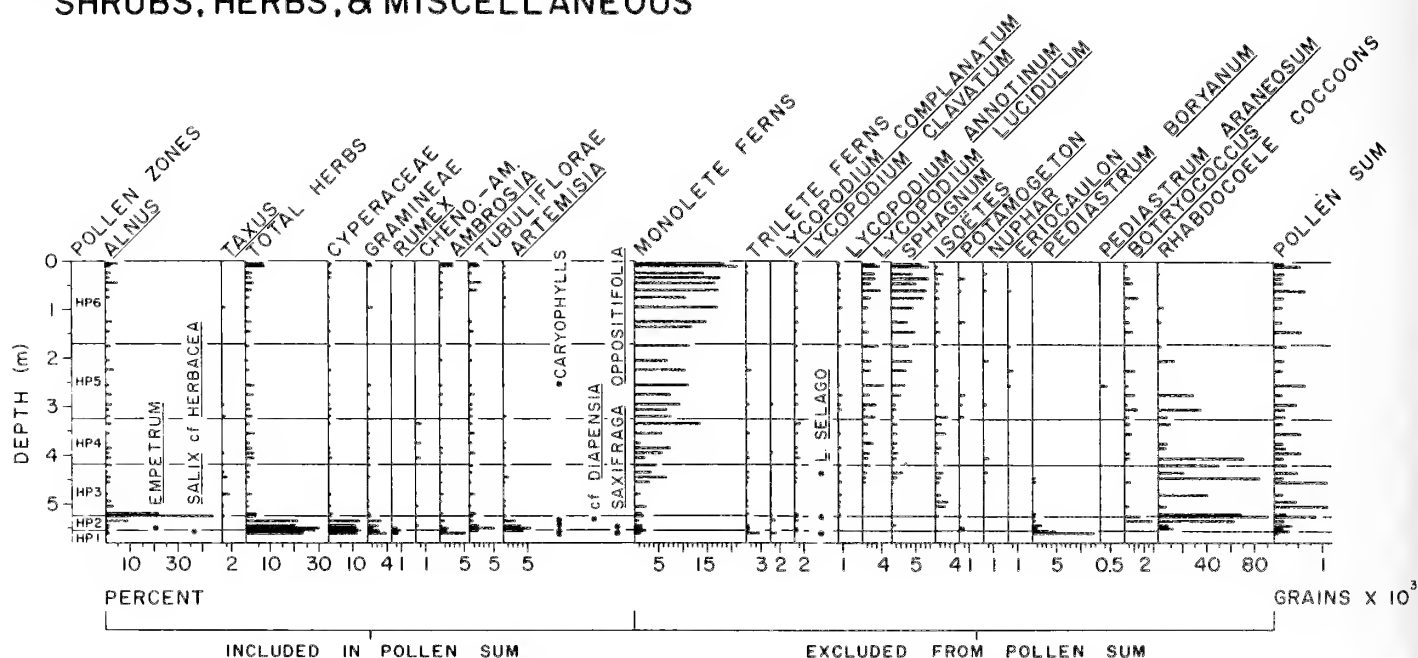


Figure 12. Lake Arnold. Pollen Diagram: Shrubs, herbs, and miscellaneous.

LAKE TEAR OF THE CLOUDS

ARBOREAL POLLEN

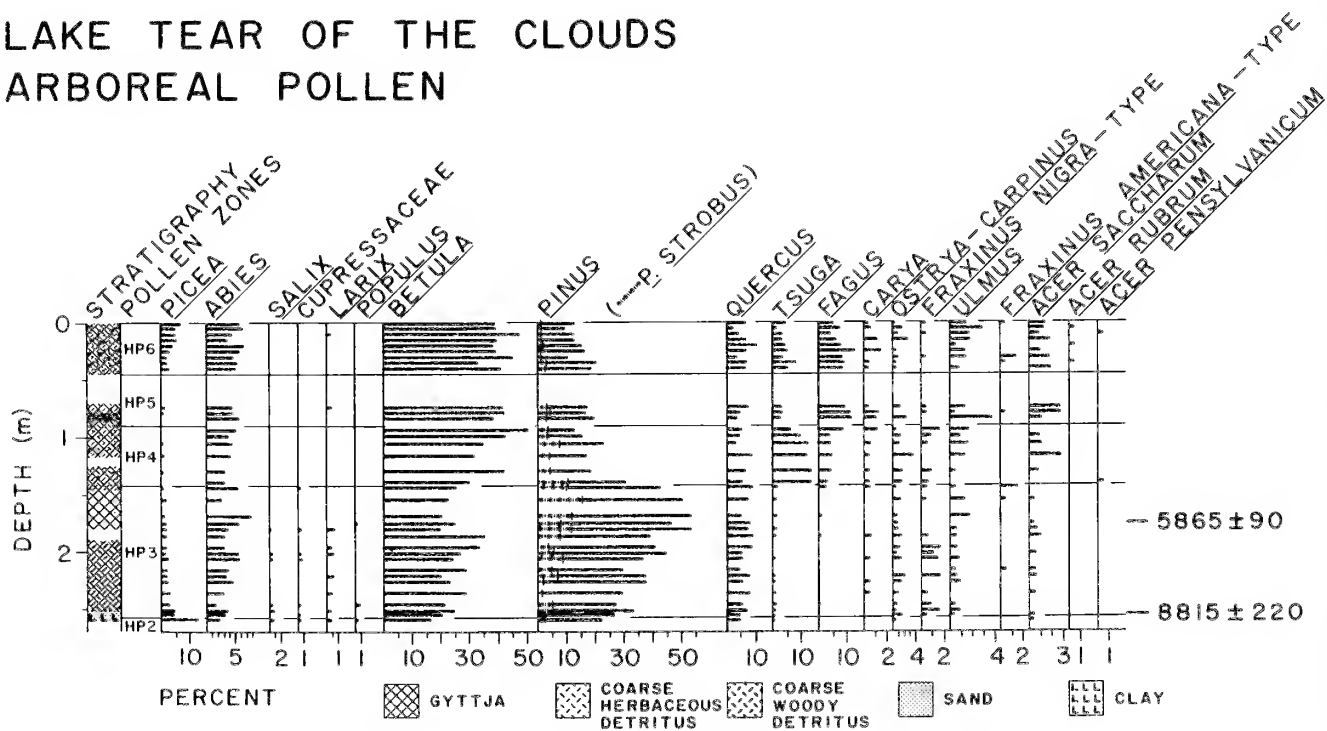


Figure 13. Lake Tear of the Clouds. Pollen Diagram: Arboreal pollen.

LAKE TEAR OF THE CLOUDS

SHRUBS, HERBS, & MISCELLANEOUS

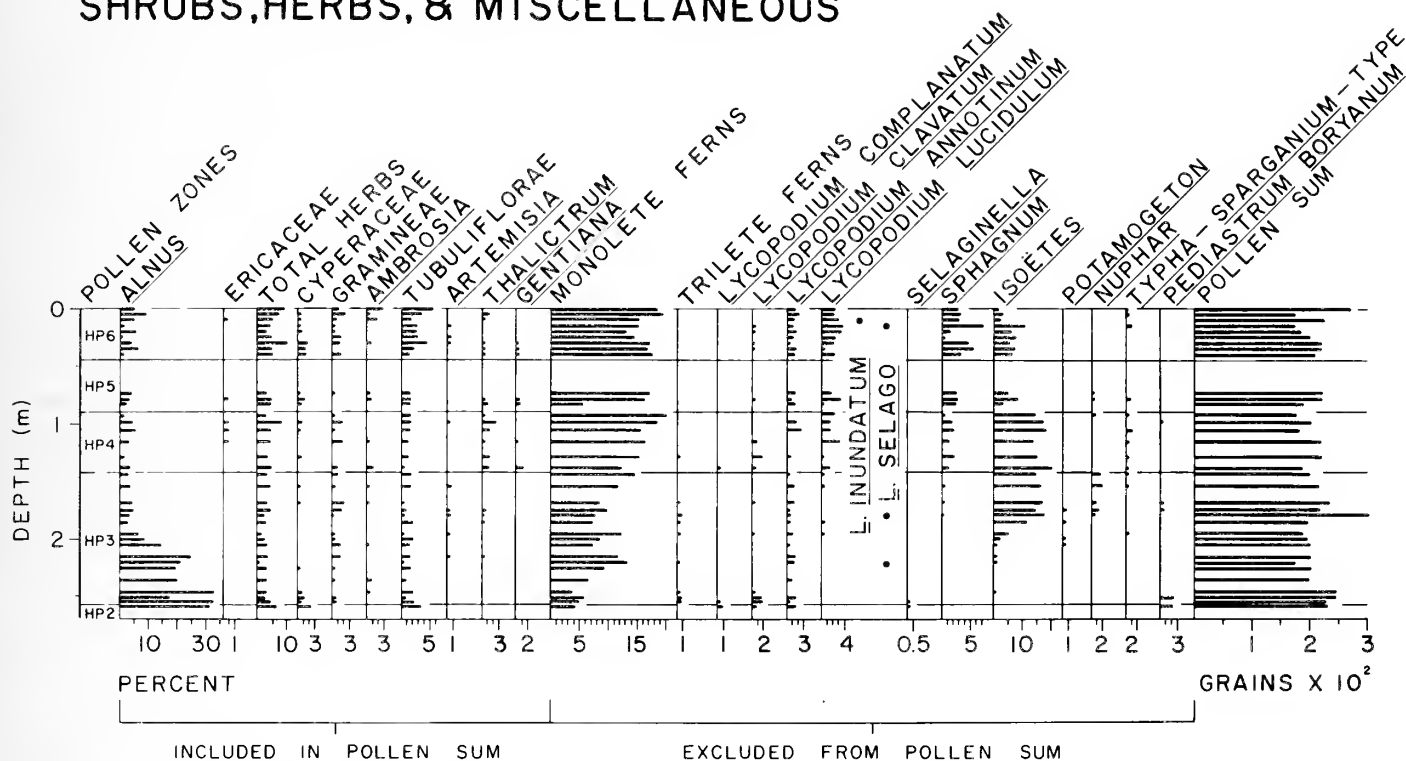


Figure 14. Lake Tear of the Clouds. Pollen Diagram: Shrubs, herbs, and miscellaneous.

LAKE ARNOLD

LAKE ARNOLD

BETULA MEASUREMENT

DIPLOXYLON PINE MEASUREMENT

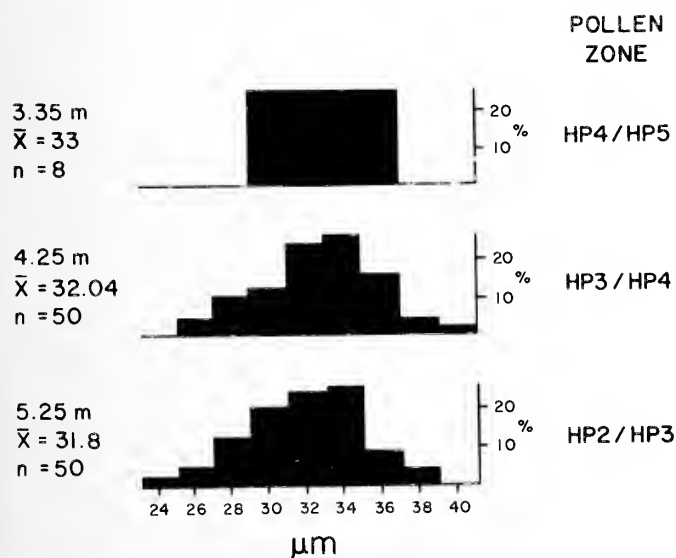


Figure 15. Lake Arnold. Measurements of Diploxylon pine pollen from selected levels.

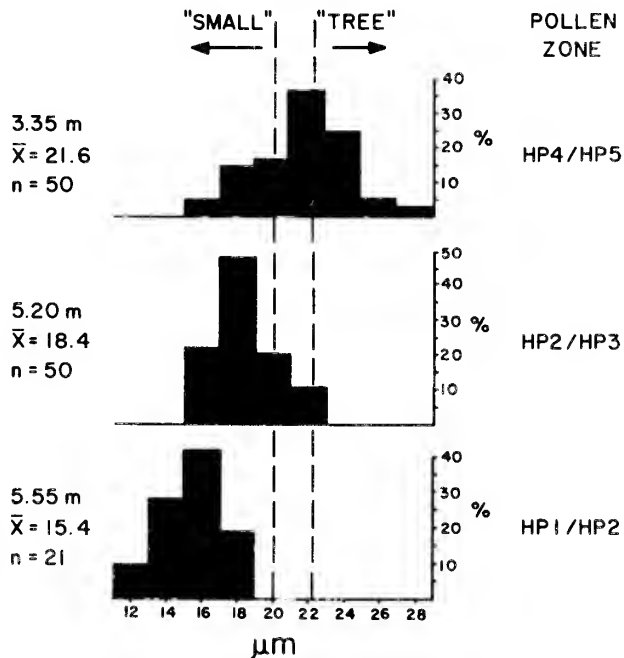


Figure 16. Lake Arnold. *Betula* measurements from selected levels.

MODERN ANALOGS FOR FOSSIL POLLEN ASSEMBLAGES

We attempted to find the modern pollen assemblages most similar to representative fossil spectra from each assemblage zone from the Heart Lake and Upper Wallface Pond profiles. Jonathan T. Overpeck carried out the analysis with a computer program that he developed using an algorithm technique described by Overpeck *et al.* (1985). A dissimilarity coefficient was calculated between each fossil spectrum and each of 1800 modern pollen spectra representing all of the major vegetation types in northeastern North America. Fourteen dominant arboreal pollen types were used for comparisons. The chord distance dissimilarity coefficient was used as it eliminates some of the bias caused by overrepresentation of some pollen types (Overpeck *et al.* 1985). The results are presented in Tables 3 and 4.

The closest matches for spectra from HP-1 and HP-2

(13,000-9700 yr BP) are from the boreal forest in northeastern North America north of 48°N latitude and east of 80°W longitude. However, it is important to note that herb-pollen types were not included among the 14 pollen types used to calculate chord distances. Herb-pollen percentages for pollen zones HP-1 and HP-2 indicate that the best matches are from modern tundra and forest-tundra.

The closest modern analogs for the *Pinus* zone (9700-7000 yr BP) are mixed conifer and hardwood forest in the upper midwest (northern Michigan and adjacent Wisconsin). The best analogs for the upper three pollen zones (7000-present) are mixed forest in the Northeast (the Adirondack region), southern Ontario, and adjacent northern New England). The youngest Holocene samples (within Zone HP-6) are all most similar to modern samples from the Adirondack region.

Table 3
Heart Lake—Modern Analogs for Fossil Spectra

Depth (cm)	Pollen Zone	¹⁴ C Age (yr BP)	Best Modern Analog		Minimum Squared Chord Distance	Veg. Type
			Lat.	Long.		
0	HP6	0	44.183	73.967	0.0234	Mixed Forest (NY)
10	HP6	250	44.267	71.317	0.0312	Mixed Forest (NY)
30	HP6	600	44.050	74.950	0.0262	Mixed Forest (NY)
50	HP6	950	44.183	73.967	0.0310	Mixed Forest (NY)
70	HP6	1200	44.050	74.950	0.0249	Mixed Forest (NY)
90	HP6	1400	44.050	74.950	0.0213	Mixed Forest (NY)
110	HP6	1600	44.050	74.950	0.0360	Mixed Forest (NY)
130	HP6	1800	44.050	74.950	0.0344	Mixed Forest (NY)

Table 3 (cont.)
Heart Lake—Modern Analogs for Fossil Spectra

Depth (cm)	Pollen Zone	¹⁴ C Age (yr BP)	Best Modern Analog		Minimum Squared Chord Distance	Veg. Type
			Lat.	Long.		
150	HP5	1950	44.133	74.433	0.0636	Mixed Forest (NY)
170	HP5	2100	44.400	74.283	0.0549	Mixed Forest (NY)
190	HP5	2300	43.433	74.500	0.0682	Mixed Forest (NY)
220	HP5	2600	44.133	74.433	0.0845	Mixed Forest (NY)
240	HP5	2800	44.867	72.150	0.0871	Mixed Forest (NY)
270	HP5	3150	44.400	74.283	0.0833	Mixed Forest (Quebec)
290	HP5	3400	43.433	74.500	0.0860	Mixed Forest (NY)
335	HP5	3900	44.133	74.200	0.0727	Mixed Forest (NY)
365	HP5	4300	43.867	74.167	0.0563	Mixed Forest (NY)
375	HP5	4400	43.867	74.167	0.0737	Mixed Forest (NY)
385	HP5	4600	45.961	73.867	0.0544	Mixed Forest (Quebec)
410	HP4	5000	41.833	77.950	0.0903	Mixed Forest (PA)
440	HP4	5500	43.550	73.817	0.0770	Mixed Forest (NY)
490	HP4	6400	44.983	84.300	0.0613	Mixed Forest (MI)

Table 3 (cont.)
Heart Lake—Modern Analogs for Fossil Spectra

Depth (cm)	Pollen Zone	¹⁴ C Age (yr BP)	Best Modern Analog		Minimum Squared Chord Distance	Veg. Type
			Lat.	Long.		
540	HP3	7600	44.983	84.300	0.0501	Mixed Forest (MI)
580	HP3	8750	45.083	84.150	0.0330	Mixed Forest (MI)
610	HP3	9700	46.033	89.683	0.0395	Mixed Forest (WI)
620	HP2	10,000	48.583	78.183	0.0410	Conifer Forest (Quebec)
632	HP2	10,500	47.417	71.200	0.1196	Conifer Forest (Quebec)
640	HP1	10,900	47.417	71.200	0.1677	Conifer Forest (Quebec)

Table 4
Upper Wallface Pond—Modern Analogs for Fossil Spectra

Depth (cm)	Pollen Zone	¹⁴ C Age (yr BP)	Best Modern Analog		Minimum Squared Chord Distance	Veg. Type
			Lat.	Long.		
0	HP6	0	44.050	74.950	0.0513	Mixed Forest (NY)
20	HP6	300	44.050	74.950	0.0508	Mixed Forest (NY)
57	HP6	900	45.961	73.867	0.0493	Mixed Forest (Quebec)
87	HP6	1500	43.433	74.500	0.0559	Mixed Forest (NY)
105	HP6	1900	45.961	73.867	0.0686	Mixed Forest (Quebec)

Table 4 (cont.)
Upper Wallface Pond—Modern Analogs for Fossil Spectra

Depth (cm)	Pollen Zone	¹⁴ C Age (yr BP)	Best Modern Analog		Minimum Squared Chord Distance	Veg. Type
			Lat.	Long.		
135	HP5	2900	45.533	73.150	0.0561	Mixed Forest (Quebec)
155	HP5	3800	45.533	73.150	0.0685	Mixed Forest (Quebec)
165	HP5	4200	45.961	73.867	0.0779	Mixed Forest (Quebec)
175	HP4	4800	45.961	73.867	0.0880	Mixed Forest (Quebec)
203	HP4	5600	45.567	75.917	0.0779	Mixed Forest (Quebec)
240	HP4	6600	44.633	68.633	0.0540	Mixed Forest (ME)
277	HP3	7200	46.033	89.167	0.0416	Mixed Forest (WI)
303	HP3	7750	43.983	70.350	0.0580	Mixed Forest (ME)
333	HP3	8500	46.033	89.167	0.0374	Mixed Forest (WI)
371	HP3	9850	45.800	79.450	0.0787	Mixed Forest (Ontario)
381	HP3	10,200	47.550	71.250	0.0866	Mixed Forest (Quebec)
403	HP2	11,000	48.583	78.183	0.0513	Conifer Forest (Quebec)
413	HP2	11,500	49.067	80.600	0.0624	Conifer Forest (Ontario)
483	HP1	12,500	48.333	80.500	0.0560	Conifer Forest (Quebec)

VEGETATIONAL HISTORY

Vegetational Development from Ice Retreat to about 12,000 yr BP

Extrapolation of the oldest radiocarbon dates from both Heart Lake and Upper Wallface Pond suggests that these basins were ice-free by at least 12,500 yr BP, and probably by 13,000 yr BP. This suggestion is consistent with the geological evidence for deglaciation of the Adirondacks cited earlier (Craft 1979, Denny 1974, Denton and Hughes 1981). Although detailed geologic studies and more radiocarbon dates are needed, the High Peaks region was probably deglaciated by 13,000 radiocarbon years ago.

The oldest pollen assemblages from Heart Lake, Upper Wallface Pond, and Lake Arnold are similar and probably derive from an essentially treeless vegetation, probably tundra, as indicated by the high percentage of herb pollen, the presence of pollen or spores of assumed tundra taxa (e.g., *Empetrum*, *Diapensia*, a variety of caryophylls, *Salix* cf. *herbacea*, *Lycopodium selago*, *Saxifraga oppositifolia*-type), low pollen deposition rates, and plant macrofossil evidence (Jackson 1983, 1990). However, the presence of *Picea* needles in HP-1 at Heart Lake indicates that scattered *Picea* trees were present (Jackson 1983, 1990).

The pollen spectra suggest that the vegetation consisted of grasses, sedges, a variety of Compositae (e.g., *Artemisia*, *Ambrosia*), *Rumex*, and *Salix*. The other tundra taxa mentioned above were also present, at least locally.

The high percentages of *Pinus* pollen and presence of pollen of deciduous trees (*Quercus*, *Carya*, *Ostrya-Carpinus*, *Fraxinus nigra*-type, and *Ulmus*) is undoubtedly an artifact of the low pollen productivity of tundra and long-distance transport of tree pollen from the south. *Betula* pollen might also be explained in this manner or alternatively may reflect the presence of shrubby-tundra species (pollen measurements suggest that at least some of the pollen was derived from shrub-*Betula* species—see Fig. 16). For example, *Betula glandulosa*-type leaf fragments occur in HP-1 at Heart Lake (Jackson 1983, 1990).

The Development of Boreal Woodland (about 12,000-9700 yr BP)

Picea was the first tree taxon to immigrate into the High Peaks region; the presence of *Picea* needles in HP-1 at Heart Lake indicates that some individuals were present before 12,000 yr BP, at least at lower elevations (Jackson 1983, 1990). *Salix* (presumably shrub species), *Juniperus* ("Cupressaceae" pollen), and *Abies* all appear to have immigrated and colonized shortly after *Picea*. Macrofossils indicate local presence of *Larix* after 11,000 yr BP and *Abies* after 10,500 yr BP (Jackson 1983). *Populus* immigrated about 10,000 yr BP, coinciding with a sharp decline of *Picea*.

Picea populations appear to have spread rapidly at all elevations after 12,000 yr BP. The resulting *Picea*-dominated vegetation had an interrupted canopy, or it contained significant treeless patches. Supporting this conclusion are the low pollen deposition rates, the continuing high percentages of most of the herb types represented in HP-1, the persistence of macrofossils of some tundra species (Jackson 1983, 1990), and the strong representation of fern and certain club moss spores (notably *Lycopodium annotinum*, *L. complanatum*-type, and *L. clavatum*).

Some deciduous trees may have been present in this boreal woodland/parkland. Distinct maxima occur for *Ostrya-Carpinus*, *Fraxinus nigra*-type, and *Ulmus* early in HP-2 at Heart Lake. The pollen percentages for these taxa are highest at Heart Lake, suggesting that if present, they were restricted to lower elevations. These species are among those that Davis and Jacobson (1985) refer to as "secondary invaders" in New England (arriving in that area after *Populus*, *Picea*, *Betula papyrifera*, and *Pinus banksiana*). However, the high percentages of these deciduous taxa during late-glacial time may result from long-distance transport. M.B. Davis (1981b) discusses the difficulty of determining exactly when *Ostrya* and/or *Carpinus* arrived in New England.

Picea began to decrease rapidly at all sites about 10,500 yr BP, probably in response to climatic warming. The *Picea* decline was accompanied by rapid expansion of *Alnus* populations (*Alnus crispa* based on both pollen and macrofossils). The *Alnus* maximum is evident at all sites, but it is more pronounced and persists longer at higher elevations. An expansion of *Abies* and *Larix* and the immigration and spread of *Populus* also coincide with the *Picea* decline.

Alnus began to decline at all sites about 10,000 yr BP, although *Alnus* was abundant until at least 7000 yr BP at Lake Tear of the Clouds. By 9700 yr BP closed forests had developed at low- and mid-elevation. *Betula* (probably *Betula papyrifera*) and *Pinus* (including *Pinus strobus*) contributed to this forest development. Macrofossil profiles record the immigration and expansion of *Betula papyrifera* at this time (Jackson 1983, 1990).

These vegetational changes are of considerable interest, because (1) they differ in several important respects from those observed at many sites in New England (see, for example, Davis and Jacobson 1985) and (2) they suggest that *Alnus* may have played a pivotal role in controlling vegetation structure and dynamics in the High Peaks between 10,500 and 9700 yr BP.

For example, *Populus*, *Alnus*, and *Larix* appear to have arrived in Maine earlier than in the High Peaks. In addition, *Alnus* was apparently present before the immigration of *Picea* into Maine.

Alnus crispa is an important early successional plant in recently deglaciated areas in Alaska and northwestern Canada

(Crocker and Major 1955, Lawrence *et al.* 1967, Ugolini 1968, Van Cleve *et al.* 1971). *Alnus* may initiate biogeochemical changes in soils that strongly influence the successional chronosequences studied. The most important of these changes are sharp increases in soil nitrogen and decreases in soil pH. The increasing availability of nitrogen may have facilitated the development of closed mixed forest in the High Peaks.

Although climatic warming and increasing soil stability may have been the primary factors contributing to the development of closed forests at the late-glacial—Holocene boundary in the High Peaks (Jackson 1990), nutrient changes related to *Alnus* may also have played a role. The higher-elevation sites have thinner soils, lower rates of weathering and mineralization, and higher runoff (Vitousek 1977), all of which would contribute to nutrient deficiencies. Thus, symbiotic nitrogen fixers such as *Alnus* would have a competitive advantage on such sites and could cause biogeochemical changes that would facilitate tree growth. Significant water-chemistry and trophic changes are recorded at about 10,000 yr BP in Heart Lake, Upper Wallface Pond and Lake Arnold. These changes coincide with changes in watershed soils and vegetation. *Alnus* may have played a role in driving these changes (Whitehead *et al.* 1986, 1989).

Early Holocene Forest Changes (9700-7000 yr BP)

The pollen changes within the *Pinus* assemblage zone (HP-3) record the development of mixed conifer-hardwood forests in the region and the immigration of many important forest trees. Among the more significant changes are (1) the striking decrease in regional abundance of *Picea*, (2) the increasing importance of *Betula* (evidently *Betula papyrifera*; Jackson 1983, 1990), (3) the immigration and rapid expansion of *Pinus strobus* populations at about 9000 yr BP, and (4) the arrival in the region of *Acer saccharum*, *Tsuga*, and *Fagus* between 8000 and 7000 yr BP. Several other deciduous trees may have been present at lower elevations in the High Peaks region during this time interval, although precise arrival times cannot be determined. Included in this category are *Quercus*, *Fraxinus*, *Ostrya-Carpinus*, *Ulmus*, *Acer rubrum*, and *Acer spicatum*.

Initially, the dominant conifer was *Pinus strobus* (with *Abies* important locally and at higher elevations), but by 7000 yr BP *Pinus strobus* had decreased, and *Tsuga* populations were expanding rapidly. *Acer saccharum* and *Fagus* became progressively more abundant as *Pinus strobus* declined.

Although pollen diagrams from each of these sites contain a significant regional component, some subtle elevational patterns are present. *Pinus strobus*, *Tsuga*, and most deciduous trees are less well represented at the higher elevation sites where *Betula* and *Abies* pollen are more abundant. Percentages of herb pollen and fern spores are also higher at Lake Tear and Lake Arnold. This suggests a gradient, with *Abies-Betula* forest at higher elevations and mixed coniferous-decid-

uous forests with *Pinus strobus*, *Tsuga*, *Acer*, *Fagus*, and other hardwoods at lower elevations (Jackson and Whitehead 1990).

The Development of *Tsuga-Pinus strobus*-Northern-Hardwoods Forests (7000-4800 yr BP)

Tsuga increased rapidly in abundance about 7000 yr BP, becoming the dominant forest tree at lower elevations. Between 7000 and 4800 yr BP, *Tsuga* pollen percentages from Lake Arnold, Wallface and Heart Lake are higher than those in any of the 60 surface sediment samples that we have analyzed from throughout the Adirondack region. Hence, we infer that *Tsuga* was much more abundant in the region than at present. *Betula*, *Fagus*, and *Acer saccharum* also increased in abundance during this period. The macrofossil record indicates that *Betula lutea* immigrated during this interval (Jackson 1990). Thus, by this time the forests contained all of the major tree species of the modern *Tsuga-Pinus strobus*-northern hardwoods forests.

The data from all four sites suggest that *Lycopodium lucidulum* became established at or slightly before 7000 yr BP. This club moss is common in rich mesic sites in northern hardwoods forests in the Adirondacks and is especially common in *Tsuga* stands. *Tsuga* probably created forest floor conditions conducive to growth of *L. lucidulum*.

An elevational gradient continued to be evident. The forests near Lake Tear and Lake Arnold were still dominated by *Abies* and *Betula* with more ferns and herbs than at lower elevations. Lower areas supported the *Tsuga*-dominated forests described above.

The *Tsuga* Decline, Development of Hardwood Forests, and Recovery of *Tsuga* (4800-2000 yr BP)

Tsuga underwent an abrupt regional decline 4800 yr BP. This decline has been detected at this time throughout the range of *Tsuga* in northeastern North America (Davis 1981a, Webb 1982). Because the event is abrupt and not time-transgressive, it has been ascribed to biogenic causes, presumably a pathogen that spread quickly (Davis 1981a).

Thus the lower elevation forests in the High Peaks region underwent a dramatic change at this time. The dominant forest tree died out very rapidly, initiating a sequence of successional readjustments. The most immediate change was a sharp, transient expansion of *Betula*. This *Betula* maximum resulted from expansion of *Betula lutea* populations, as indicated by macrofossil data (Jackson 1983). Subsequently, both *Fagus* and *Acer saccharum* and, to a lesser extent, *Abies*, became more abundant. Thus the lower-elevation forests shifted from conifer (*Tsuga*) dominance to hardwood dominance in a very short period of time.

Undoubtedly there were significant hydrological and biogeochemical consequences from this vegetational event. Throughfall chemistry and soil characteristics and chemistry are very different under *Tsuga* and hardwood canopies (Ray-

nal *et al.* 1983, Johnson and Siccama 1979). Thus, major changes in the forest-floor environment should have occurred (e.g., decreasing organic content of soil, increasing soil pH, less acid throughfall, higher light penetration, more rapid spring snowmelt) (Chandler 1939, Nihlgård 1970, Brady 1974, Cronan *et al.* 1978, Olson *et al.* 1981). Rapid colonization by *Betula lutea* may have played an important role in restoring the hydrological balance, although soil characteristics would remain different (Vitousek 1977, Vitousek and Reiners 1975, Marks 1974).

In the Heart Lake profile, pollen percentages of *Acer pensylvanicum* began to increase as *Tsuga* declined, reached a distinct maximum about 3500 yr BP, and declined gradually as *Tsuga* began to recover after 3500 yr BP. A similar pattern can be detected in the core from Lake Arnold. The initial opening of the canopy by *Tsuga* dieback might stimulate flowering of *Acer pensylvanicum* and facilitate pollen dispersal through the trunk-space to the lake (e.g., Tauber 1967), but this effect on pollen percentages might be short-lived (until canopy closure by secondary successional processes). Because of the long-term persistence of the *Acer pensylvanicum* maximum we believe that it represents a population change rather than a physiological response or pollen dispersal phenomenon.

The increase in *Acer pensylvanicum* was probably initiated by the establishment of the species in openings created by dying *Tsuga*, as *Acer pensylvanicum* displays a gap-phase establishment strategy. Most rapid growth occurs under open canopies or in light gaps (Hibbs *et al.* 1980, Wilson and Fischer 1977, Leak 1973). In addition, Hibbs *et al.* (1980) suggest that *Acer pensylvanicum* is not an important component of stands dominated by *Tsuga*. The decline in *Acer pensylvanicum* beginning at about 3400 yr BP was probably caused by the reestablishment and expansion of *Tsuga*.

Tsuga percentages began to increase again about 3500 yr BP and they attained a maximum in the upper half of zone HP-5 (3500-2200 yr BP). Clearly, some *Tsuga* populations had recovered from the hypothesized pathogen, at least at lower elevations. However, *Tsuga* did regain its pre-decline abundance. *Abies* increases slightly as *Tsuga* became reestablished.

The higher-elevation forests which had little *Tsuga* before 4800 yr BP, probably remained unchanged during this sequence of events, with *Abies* and *Betula* remaining the dominant species near Lake Tear and Lake Arnold.

The Reappearance of *Picea* (the last 2000 years)

The present regional vegetational composition of the High Peaks region was established within the last 2000 years. Modern vegetation zones were also established about 2000 yr BP (Jackson 1990, Jackson and Whitehead 1990). *Picea*, apparently absent or rare at all elevations since about 10,000 radiocarbon years ago (Jackson 1983, 1990), re-expanded dramatically at all elevations beginning about 2000 yr BP. *Abies*

increased slightly during this interval and *Tsuga*, *Fagus*, and *Acer saccharum* decreased steadily.

Recent synoptic studies of Holocene pollen data from the Northeast indicate that *Picea* abundance increased southward steadily from 4000 yr BP to the present in response to climatic cooling (Gaudreau and Webb 1985, Webb 1988). Thus, the *Picea* increase at 2000 yr BP, evident in both New England and the Adirondack pollen diagrams may have involved an immigration of *Picea* (presumably *Picea rubens*) from the north or an expansion of established *Picea* populations (Jackson 1983, 1990).

Evidence for European settlement and land clearance is evident only in the uppermost pollen spectra from each site. Within the upper 10-15 cm of each profile there is an increase in *Ambrosia*, other Compositae, several introduced species of *Plantago*, and a variety of other weeds. The *Ambrosia* signal is not strong, as land clearance for agriculture was not extensive owing to the highly irregular topography and poor soils. The *Ambrosia*-rise probably dates to about 1860 for the High Peaks region.

Local Changes in Aquatic and Wetland Vegetation

Lake Tear of the Clouds

Lake Tear of the Clouds has undergone significant changes in character during the Holocene (Fig. 13, 14; Jackson 1983). *Isoetes* microspores became abundant about 8000 years ago and then declined slightly beginning at approximately 5000 yr BP. *Sphagnum* spores were present after about 8000 years ago and increased steadily to the surface. Macrofossils of *Sphagnum*, *Viola*, *Carex*, and undifferentiated Cyperaceae also became abundant after 8000 yr BP (Jackson 1983). This suggests that Lake Tear was deeper and/or had a greater surface area in the early Holocene and that the extensive wetland area began to develop gradually about 8000 years ago. These changes might have been stimulated by changes in the lake's hydrologic budget (for example during the Hypsithermal) or they may have resulted from gradual shoaling caused by sediment accumulation.

Lake Arnold

A developmental sequence similar to that of Lake Tear of the Clouds is evident in the pollen diagrams from Lake Arnold (Fig. 11, 12), suggesting a gradual shoaling and the formation and expansion of boggy wetlands. *Isoetes* microspores are common between 9700 and 4800 yr BP. *Sphagnum* percentages increase steadily from about 4800 yr BP to the present (Fig. 12). This sequence may have been controlled by climatically induced changes in hydrology or by the gradual infilling of the basin. The gradual decrease in *Rhabdocoele* cocoons (Fig. 12) may also record steadily decreasing water depth.

However, other stratigraphic data (diatoms, *Pediastrum*, pigments, sediment chemistry) (Whitehead *et al.* 1986, 1989,

Reed 1982) (Fig. 12) indicate that Lake Arnold has undergone significant changes in lakewater chemistry and trophic status during the late Pleistocene and Holocene. These changes could also have influenced *Isoetes*, *Rhabdocoeles*, and the dynamics of wetland development. For example, during late-glacial time Lake Arnold was moderately alkaline (pH 7.5-8.0) and more productive than at present (Whitehead *et al.* 1986, 1989). Productivity peaked between about 11,000 and 9000 yr BP. The lake acidified steadily during the early Holocene and has been below pH 5.0 since 8500 yr BP. Increasing acidity may have affected the *Rhabdocoeles* and facilitated colonization of the lakeshore by *Sphagnum*.

This generalized temporal pattern for acidity and trophic status is also evident at Heart Lake and Upper Wallface Pond (Whitehead *et al.* 1986, 1989, Reed 1982).

CLIMATIC INFERENCES

We suggest that conditions immediately after ice retreat (> 13,000-11,000 yr BP) were probably comparable to those in modern tundra communities in eastern North America (July mean 10°C or less, January mean 5°C). The general climatic trend indicated by the pollen data until the early Holocene (about 7000 yr BP) was steady warming, although short-term climatic fluctuations may not be evident in the pollen record (Wright 1984). Conditions during the development of woodland/parkland (Zone HP-2; 11,000-9700 yr BP) were probably comparable to those characteristic of areas of forest-tundra east of Hudson Bay between 55-48°N latitude, based on the modern pollen analogs. Similarly, climate between 9700 and 7000 BP may have been comparable to modern conditions in areas of mixed coniferous-deciduous forest in northern Michigan and adjacent Wisconsin. The development of *Tsuga*-dominated forests between 7000 and 4800 years ago probably took place in a climatic regime like that now existing in broad areas of the Northeast, although initially the biotic environment differed because *Betula lutea* was not yet present. The macrofossil records from both New Hampshire (Davis *et al.* 1980) and the High Peaks (Jackson 1983, 1990) indicate that conditions during the early and mid-Holocene were warmer and possibly drier than at present, resulting in an upward displacement of the upper elevational limit of a number of important tree taxa. The pollen record from the High Peaks provides little insight into this phenomenon because the regional component of the pollen rain masks such elevational displacements (Jackson and Whitehead 1990).

The expansion of *Picea* within the past 2000 years was probably related to climatic cooling. This is consistent with evidence of comparable vegetational changes elsewhere in the Northeast (Davis *et al.* 1980, Webb *et al.* 1983).

COMPARISONS WITH OTHER STUDIES IN THE NORTHEAST

A number of pollen sites on the Allegheny Plateau and on

the Lake Ontario Plain in western New York (Miller 1973, 1988, Spear and Miller 1976, Calkin and McAndrews 1980) provide interesting contrasts with the High Peaks. The location, glacial geology, and topographic setting suggests that at least some facets of vegetational history in the High Peaks may have been different from those in neighboring areas. Topography, lower elevation (450-520 m) and earlier deglaciation (the record for Belmont Bog may extend back to > 16,000 yr BP; Spear and Miller 1976) may have allowed at least some of the important colonizers to immigrate earlier than in the High Peaks.

The overall vegetational trends on the Allegheny Plateau are similar to those detected in the High Peaks and elsewhere in the Northeast. Pollen zones similar to those described for the High Peaks sites are detectable in virtually every Allegheny Plateau profile.

Some interesting and predictable differences do exist. For example, the period of tundra-like vegetation inferred from the Belmont Bog profile extends for a much longer time period (> 16,000 to 12,500 yr BP). If tundra-like conditions lasted for nearly 4000 years following ice retreat in western New York, then climate rather than migrational lag was responsible for the conditions prior to 12,000 yr BP in the High Peaks. Not surprisingly, *Picea* and probably *Pinus banksiana* became established near the Allegheny Plateau sites at least 500 years earlier than in the High Peaks.

The sequence of vegetational changes for the remainder of the late Pleistocene and Holocene parallels that for the High Peaks region, with some significant differences, however. *Fagus* and *Quercus* were more important, and *Betula*, *Tsuga*, *Abies*, and *Picea* less important on the Allegheny Plateau. The re-expansion of *Picea* characteristic of the last 2000 years in the High Peaks is virtually undetectable on the Allegheny Plateau. *Picea rubens* does not occur on the Allegheny Plateau, and *P. mariana* populations are restricted to scattered, small peatlands.

Inadequate radiocarbon control for the Allegheny Plateau sites precludes precise comparison of immigration times for various species, although the general sequence of appearance was comparable to the High Peaks, and different from that recorded in adjacent parts of New England (R.B. Davis and Jacobson 1985). For example, both *Alnus* and *Larix* arrived on the Allegheny Plateau after the immigration and establishment of *Picea*.

Recent studies of the sediments of Brandreth Bog at 600 m elevation, about 90 km southwest of the High Peaks, provide detailed, carefully dated information on the developmental history of an Adirondack bog and the vegetational history of the surrounding region (Overpeck 1985). The vegetational history spans the time interval from > 10,500 yr BP to the present and records a sequence of vegetational changes similar to that of the High Peaks. Given the proximity of Brandreth Bog to the High Peaks sites, it is not surprising that its pollen stratigraphy is intermediate between that of sites on the Allegheny Plateau and those in the High Peaks region. For example, percentages of *Picea*, *Abies*, and *Tsuga* are higher

than those in the Allegheny Plateau (but lower than the High Peaks); percentages of *Betula* are still lower than the High Peaks. The late-Holocene expansion of *Picea* is evident in the Brandreth Bog diagram, but it occurred 500-1000 years later than in the High Peaks. Given the time-transgressive pattern of *Picea* expansion from areas north of the St. Lawrence River suggested by Webb *et al.* (1983), some delay would be expected.

The Adirondack sequences are also similar to those inferred from many sites in New England (e.g., Anderson *et al.* 1986; Davis 1969, 1981b; R.B. Davis *et al.* 1975; R.B. Davis and Jacobson 1985; Whitehead 1979). The overall trend from tundra to *Picea* woodland to mixed conifer-deciduous forest to northern hardwoods (with an important role for *Tsuga* from about 8000 to 4800 yr BP), a sharp decline of *Tsuga* at 4800 yr BP (M.B. Davis 1981a), and onset of cooler conditions by 2000 yr BP (often indicated by an expansion of *Picea*) are found in virtually all complete profiles from the northern half of New England (M.B. Davis 1983, R.B. Davis and Jacobson 1985). However, important differences do exist in the relative abundance of particular tree taxa and the order in which taxa immigrated (or colonized).

In northern New England the "advanced invader" (R.B. Davis and Jacobson 1985a) appears to have been *Populus*; in the High Peaks, *Picea* and *Salix*. The "primary invaders" in New England were *Picea*, *Betula papyrifera*, and *Pinus banksiana*; in the Adirondacks they included *Abies*, *Larix*, *Fraxinus*, cf. *Juniperus*, *Ostrya-Carpinus*, and *Pinus banksiana*. The "secondary invaders" in New England were *Ostrya-Carpinus*, *Fraxinus nigra*-type, *Abies*, *Larix*, and *Ulmus*; in the High Peaks they included *Betula papyrifera*, *Populus*, and *Fraxinus americana*. Tertiary invaders in New England included *Quercus*, *Acer*, *Pinus strobus*, and *Tsuga*; in the High Peaks the later invaders included *Quercus*, *Acer saccharum*, *Pinus strobus*, *Tsuga* and *Fagus*. Many of these dif-

ferences may reflect differential immigration rates into the two regions (resulting from different migration routes or from different regional climate patterns), although some may be statistical artifacts (e.g., M.B. Davis 1981b, R.B. Davis and Jacobson 1985, Jackson 1990). Clearly, many problems are associated with interpretation of the late-glacial and early Holocene pollen percentages for *Larix*, *Ostrya-Carpinus*, *Fraxinus*, *Ulmus*, *Quercus*, and *Populus*. Significant long distance transport may have contributed to the late-glacial and early Holocene increases for these taxa.

A combination of pollen and macrofossil data clearly indicates that *Betula lutea* and *Alnus* behaved very differently in the High Peaks and New England. *Alnus* colonized tundra vegetation early in the late Pleistocene at low elevations in New England, whereas it appears to have been delayed significantly in the Adirondacks. Its appearance and spread in the Adirondacks coincides with the decline of *Picea* (and deterioration of *Picea* woodlands) at about 10,000 yr BP. The *Alnus* involved in both regions was *Alnus crispa* (Jackson 1983, 1990, R.B. Davis and Jacobson 1985). Similarly, *Betula lutea* did not become established in the High Peaks until about 6000 yr BP (Jackson 1983), whereas it was present much earlier in New Hampshire (Spear 1981) and Maine (Anderson *et al.* 1986). The rugged topography and isolated position of the Adirondacks may have contributed to the delayed immigration of these taxa. Pollen and macrofossil studies at lower elevations in the eastern Adirondacks are needed to explore this hypothesis.

Although many of the vegetational contrasts between the High Peaks and areas to the west and east seem clear, it is obvious that many gaps exist in our knowledge. The actual pattern of immigration into the Adirondacks will only be established when detailed work is carried out in the Hudson-Champlain lowlands, in the Mohawk Valley, and in the more subtle topography of the western Adirondacks.

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